Melanoides rhizoporarum (A. Potamides sulcatus (Born) Adams) "palustris (Linnaeus)

Lilimbon River, near source, Marivelles, Luzon

Brotia asperata
(Lamarck)

Melanoides aculeus (Lea)

"crenulata
(Deshayes)

"hastula (Lea)

"lateritia (Lea)

Lilimbon River, 20-25 ki. from source

Lilimbon River, near mouth

Antipode River, tributary of Pasig River, Luzon

Brotia asperata (Lamarck) Pila scutala (Mousson)

TRANSPOSED HINGE TEETH OF NORTH AMERICAN NAIADES

BY HENRY VAN DER SCHALIE

In connection with my work of the past few years, which was concerned largely with studies of our American freshwater mussels, I observed a number of variations in the tooth-structure of the hinge. I had accumulated quite a series of such variations when I noted a paper on the subject by Popenoe and Findlay. These men in their paper on "Transposed Hinge Structures in Lamellibranchs" have not only accumulated an interesting series

of variations, but have also contributed an excellent bibliography of the literature bearing on this subject. Since their work is so largely concerned with variations in both recent and fossil marine forms, rather than freshwater forms, I felt that it would be well to mention some of the variations observed in our freshwater mussels.

One of the earliest published observations regarding a transposed hinge is that of Louis Agassiz who in 1859 exhibited a specimen of *Unio ligamentinus* (Actinonaias carinata) at a meeting of the Boston Society of Natural History. Agassiz mentioned that he thought it was rare and not easily observed. Mr. Isaac Lea, when he noticed Agassiz's communication to the society, published a list in 1860 of the specimens he had observed to indicate such abnormalities. I have revised Mr. Lea's list according to our present system of nomenclature and have listed the North American forms he mentions there:

Transposed Hinge Teeth of North American Naiades Reported by Isaac Lea in 1860, Proc. Acad. Nat. Sci., p. 51

Single lateral in each valve:

Elliptio complanatus (Dillwyn)

2 Lampsilis ventricosa (Barnes) Proptera purpurata (Lamarck)

Single lateral in left; double in right:

Elliptio hopetonensis (Lea)

2 Elliptio complanatus (Dillwyn)

Proptera alata (Say)

Ligumia nasuta (Say)

Lampsilis radiata (Gmelin)

Double lateral in both valves:

3 Elliptio complanatus (Dillwyn)

Treble lateral in left valve; partly treble in right: Elliptio dilatatus (Raf.)

Three Uniones have been omitted from the above list, since they are not North American, two being from India and one from Bengal.

In this connection I have prepared the following tables to indicate the series of specimens and their variations which I have observed:

RECORDS OF TRANSPOSED HINGE TEETH OF NORTH AMERICAN NAIADES

Single lateral in each valve:

Amblema costata (Raf.) Mich. Fusconaia flava (Raf.) Mich. Elliptio strigosus (Lea) Georgia

2 Elliptio obnubilus (Lea) " (2 lots) Plectomerus dombeyana (Val.) Miss.

11 Micromya iris (Lea) Mich. (8 lots)

2 Micromya vibex (Conrad) Florida

5 Ligumia nasuta (Say) Mich. (3 lots) 2 Lampsilis fasciola (Raf.) Mich. (2 lots)

5 Lampsilis siliquoidea (Barnes) Mich. (4 lots)

2 Lampsilis anodontoides (Lea) Ky.

Single lateral in left valve; double in right:

3 Elliptio strigosus (Lea) Georgia (2 lots)
Elliptio obnubilus (Lea) "
Micromya iris (Lea) Mich.
Micromya viber (Conned) Coorgia

Micromya vibex (Conrad) Georgia 2 Micromya lienosa (Conrad) Florida

Ligumia nasuta (Say) Mich. Lampsilis fasciola (Raf.) Mich.

2 Lampsilis siliquoidea (Barnes) Mich. (2 lots) Lampsilis claibornensis (Lea) Miss.

Double lateral in both valves:

Fusconaia flava (Raf.) Mich.

Amblema boykiniana (Lea) Georgia

4 Elliptio dilatatus (Raf.) Mich.

3 Elliptio obnubilus (Lea) Georgia (3 lots) Elliptio folliculatus (Lea) Georgia

3 Ptychobranchus fasciolare (Raf.) Mich. (3 lots) Medionidus kingii B. H. Wright, Florida Carunculina paula (Lea) Georgia

2 Micromya iris (Lea) Mich. (2 lots) Micromya ogeecheensis (Conrad) Georgia Ligumia recta (Lamarck Mich.

6 Lampsilis siliquoidea (Barnes) Mich. (5 lots)

Triple lateral in right valve; double in left:
Micromya iris (Lea) Mich.

In general, the normal dentition in species belonging to the sub-families *Unioninae* and *Lampsilinae* is such that the lateral tooth of the left valve is double, while that of the right valve is single; with the cardinals bearing the same relationship, though

often there is a tendency for the cardinal in the right valve to double. However, as Lea (1860, p. 52) has shown, and as my tables indicate, there are many aberrant forms. Again, it is of interest in this connection to note that these have for the most part been ignored by workers in the field, and many of the descriptions of species in a manual such as Simpson's (1914): "Catalogue of the Naiades" fail to take them into account.

It is not my intention to attempt to explain just why these forms vary as they do. I merely wish to call attention to them, and to suggest that it would be of interest if we could accumulate a mass of such information which might give some clues as to whether such variations have any evolutionary significance. At present, we have based our evolutionary concepts of the North American naiades entirely on their gill structure and its modifications for the carrying of glochidia. We do not have any adequate system based on any other organ or group of organs which will substantiate what has been postulated on the basis of gill-structure. It would, therefore, be of interest if we could substantiate our present system by information such as may be furnished from hinge-structure.

That hinge-structure has been used by former workers, such as Neumayr, Bittner, von Wöhrmann, and von Vest, to trace the evolution of freshwater forms from certain marine ancestors is well known. Nevertheless, there is still a good deal of uncertainty regarding this matter. It would perhaps be well to review briefly the most important of these theories.

Neumayr, in 1889, was the first to postulate the origin of the Unionidae from the marine *Trigonia*. He pointed out that the structure of the hinge in both groups is of the schizodont type, and he also suggested that there is an affinity in the structure of the gills, the separation of the two lobes of the mantle, and in the absence of siphons. It is also indicated that there is some similarity in the development of a nacreous shell, the presence of a strong epidermis and the arrangement of the muscle scars of both groups.

S. von Wöhrmann, in 1893, agreed that there are relationships between *Unio* and *Trigonia*. He, however, believes that the naiades have descended from the marine genus *Trigonodus*. His theory, too, seems very plausible since he reports that *Trigonodus*

only occurs in sand, rubble and marls of the Raibler deposit of the Alps, the lithologic composition indicating deposition near a coast. This is also the case in *Trigonodus cristonensis* in North America. It is suggested that this proximity to the coast has permitted colonization in the mouths of rivers where the transformation into the *Unio*-like form was carried out.

W. von Vest, in 1899, postulated the origin of the Unionidae from Avicula. He believes this more plausible than from either of the two other groups. He mentions that Avicula had already appeared in Silurian time and that it has been a vigorous group from that time to the present. He believes that this genus might well have colonized rivers. He argues that the hinge-structure of Unio is already present in the embryonic forms of Avicula where it is shown by two small but prominent teeth, which could thicken in the descendants of Avicula living in rivers and thus form the powerful hinge elements of a Unio. On the other hand, the weakly developed teeth of the Avicula-hinge could disappear completely during the transformation into the freshwater forms, and in this way the toothless forms, such as Anodonta, Leila, Spatha, etc., might be developed. Again, such forms with wings, as Hyria avicularis, Hyriopsis, Proptera purpurata, etc., may be considered a reversion to the original Avicula type. Thus, in brief, is von Vest's theory. He does not ignore the previous two theories, but suggests a number of reasons why they are not tenable. In fact, he is not ready to discredit the work of Neumayr, nor that of Wöhrmann, but finds a place for their work within his own theory by stating: "It does not therefore exclude the possibility that Trigonodus itself with all its descendants, nor even Trigonia with its descendants, and likewise all Uniones in part directly, in part indirectly, might have originated from Avicula."

Not only have attempts been made to trace the evolution of bivalves on the basis of their hinge-structure, but much of our classification of this group is also based on it. Consequently, one must assume that hinge-structure is a reliable criterion because of its *constancy*. However, such an assumption is not justified unless repeated observations show that such a set of characters is constant. It is with this in mind that it would be well for us to attempt to note such variations as occur.

There is another aspect to this problem which makes a knowledge of such variations of great importance. Those working with living material are able to obtain a knowledge of variation which enables a proper evaluation of diagnostic specific characters. The paleontologist, however, is often not able to fully appreciate the significance of certain variations within groups, because of fragmentary and insufficient amount of material. Consequently, any information which can be contributed regarding the variation of certain diagnostic characters within a group ought to be of help in enabling the paleontologist to arrive at a more correct evaluation of his material.

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